dium (or *Dryopteris*). The indusium is elongate and sometimes bent, where it runs past a forking of the vein on which it is borne, as is general in *Athyrium*. It is extremely broad and thin, and completely covers the sporangia when young: The sori are then "allantodioid" (sausage-shaped). The species thus belongs to Sect. *Allantodia*, and is allied to *Athyrium umbrosum* (Aiton) Presl, of Madeira, and *Athyrium australe* (R. Brown) Presl, of Australia. The latter is the type of the genus *Allantodia* R. Brown, which was characterized largely on the shape of the indusia. The section forms a link between *Athyrium* and *Diplazium*, and its affinities need to be investigated thoroughly. The peculiar distribution (Atlantic Islands, Australia, and southern South America) suggests an ancient origin; it is not exactly paralleled among ferns, although the distributions of the genera *Pleurosorus* and *Culcita* are somewhat similar.

Cytological Observations on the Himalayan Species of Athyrium and Comments on the Evolutionary Status of the Genus*

P. N. MEHRA AND S. S. BIR

Athyrium Roth is one of the most widely distributed ferns in the Himalaya Mountains, where about 30 species occur,[1] out of a total of 180 species in the genus.[2] This number is bound to increase as the taxonomy of these ferns is better understood. Conspicuous disagreement among various authorities exists regarding the systematic position of *Athyrium*, as a survey of the various systems of classification proposed since the beginning of the present century reveals.[3] Recently, Copeland and Holttum have followed Milde[4] in uniting *Diplazium* Swartz with *Athyrium*, which has in fact added to the existing confusion, for *Athyrium* so construed (and also including *Deparia*, *Cornopteris*, and other segregates) is then a genus of about 600 species.

*Invited paper for the Fiftieth Anniversary Volume of the Journal. [Ed.]
[1]Clarke, 1880; Beddome, 1892; Hope, 1899–1904.
[2]Ching, 1940.
[3]Christensen, 1906, 1938; Bower, 1928; Ching, 1940; Dickason, 1946; Holttum, 1949; Copeland, 1947; Alston, 1956.
[4]Bot. Zeit. 1866: 373.

In the present paper the genus is treated in the traditional sense as proposed by Roth[5] and followed by Diels, Christensen, Ching, Dickason, and others.

Some species of *Athyrium* are difficult to separate morphologically from those of *Diplazium*, as for instance *A. thelypterioides* (Michx.) Desv. and *D. japonicum* (Thunb.) Beddome; the role of cytology is significant here. Cytological information is available regarding 22 clear-cut species, of which eleven are from the Himalayas,[6] five from Ceylon,[7] three from Europe,[8] two from North America,[9] and one from South India.[10] Chromosome counts show that all are based on $x = 40$. Thus on cytological grounds *Athyrium* differs consistently from *Diplazium*, which has 41 as a base number;[11] this fully justifies the retention of *Diplazium* as a genus distinct from *Athyrium*.

The present paper deals with cytological observations on 16 previously unstudied species of *Athyrium*, and with the evolutionary status of the genus.

MATERIALS AND METHODS

Fourteen species have been studied from the Eastern Himalayas, all from Sikkim State except *A. macrocarpum* (Blume) Beddome (from Darjeeling, 6,000 feet elevation[12]); the other two species are from the Western Himalayas. Material of *Athyrium pectinatum* (Wall.) Presl from both regions has been studied. The species show an altitudinal range from 3,000 to 14,000 feet. Two more species, *A. Schimperi* and *A. thelypterioides* that have already been studied from material from Darjeeling and Mussoorie respectively (Mehra and Verma, 1957) have been reinvestigated from cytogeographical considerations.

The material of four species came from the Western Himalayas. Two of these, *A. thelypterioides* and *A. dentigerum*

[5] Roem. Mag. 2[1]: 105. 1799.
[6] Mehra and Verma, 1957; Bir, 1959.
[7] Manton, 1953; Manton and Sledge, 1954.
[8] Manton, 1950.
[9] Britton, 1953; Wagner, 1955.
[10] Mahabale et al., 1953.
[11] Manton, 1954; Manton and Sledge, 1954; Brownlie, 1958; Bir, 1959.
[12] Observations by Mr. S. C. Verma.

FIG. 1, ATHYRIUM ATTENUATUM, DIPL., $n = 40$, $\times$ 500. FIG. 2, IBID., TETRAPL., $n = 80$, $\times$ 500. FIG. 3, IBID., SPORES $\times$ 150 (a, DIPL.; b, TETRAPL.). FIG. 7, DIAGRAM FROM FIG. 4. FIG. 8, DIAGRAM FROM FIG. 6. FIG. 9, SPORE MOTHER CELL, A. MEHRAE, 40 BIVALENTS, LATE DIAKINESIS, $\times$ 500. FIG. 10, A. SPINULOSUM, $n' = 80$, $\times$ 500

(Clarke) Mehra et Bir,[13] were collected near Dhanolti, along the Mussoorie-Tehri Road, at an altitude of 7,000 feet. *Athyrium thelypterioides* is a rather rare fern in this area and only a few plants were seen, growing in a clump; it is never so abundant here as in the Eastern Himalayas between 8,000 and 13,000 feet altitude. *Athyrium falcatum* Beddome is extremely rare at Nainital (7,000 feet). *Athyrium pectinatum* (Wall.) Presl is a comparatively low altitude fern; it is abundant near Mossy Falls (5,000 feet) and Sainji (3,000 feet) on the Mussoorie-Chakrata Road, where it forms extensive beds because of its creeping and branched rhizomes. Two individuals of another *Athyrium* were found near Magra (6,000 feet), on the way to Nag Tiba (Mussoorie) that are morphologically similar to *A. pectinatum;* they are suspected to be of hybrid origin, since they are cytologically abnormal, and are here designated *A.* × *pectinatum.*

The most beautiful of the Sikkim species is *A. Tsaii* Ching, which covers vast areas in the Lachen Valley at elevations between 10,000 and 12,000 feet, especially near Simdong (11,000 feet); the fronds and stipes are characteristically yellowish in colour. Another fern having almost the same distribution is *A. attenuatum* (Clarke) Tagawa. Two closely allied species with creeping rhizomes are abundant around Thangu (13,000 feet), namely *A. subtriangulare* (Hook.) Beddome, with a conspicuously yellowish lamina, and *A. spinulosum* (Maxim.) Milde, with chaffy and markedly pinkish stipes. Still higher up (14,000 feet), on the hill at the back of Thangu Dak Bungalow, *A. subtriangulare* var. *sikkimense* Bir grows occasionally under rhododendron trees in rather exposed situations. One of the rarest species is *A. Mehrae* Bir, which has very fragile fronds; only two plants were seen growing under the forest cover about two miles downwards from Thangu, at about 12,000 feet elevation, but a thorough search of the area may possibly

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[13] ATHYRIUM **dentigerum** (C. B. Clarke) Mehra et Bir, *comb. nov.* *Asplenium filix-foemina* var. *dentigera* C. B. Clarke, Trans. Linn. Soc. London, II, Bot. 1: 491. 1880.

reveal more individuals. The other species—*A. rupicola* (Hope) C. Chr., *A. parasnathense* (Clarke) Ching, *A. himalaicum* Ching, *A. Birii* Ching, *A. rubricaule* (Edgw.) Bir, *A. polysporum* (Clarke) Ching, and *A.* aff. *flabellulatum* (Clarke) Tardieu—grow at comparatively low elevations around Lachen, 8,000–9,000 feet altitude. In eastern Sikkim, *A. rupicola* attains much higher elevations, and some specimens were collected at Changu (about 13,800 feet). *Athyrium Schimperi* and *A. pectinatum* grow at still lower elevations than the other species from Sikkim reported here; they are common along the road between Chungthang and Lachen at about 6,000 feet. Full descriptions have been published only for *A. spinulosum*, *A. Schimperi*, *A. pectinatum*, *A. falcatum* and *A. macrocarpum*,[14] *A. attenuatum*,[15] *A. subtriangulare*,[16] and *A. rupicola*.[17] The taxonomic observations and complete descriptions of the others, which are either new species or varieties or new combinations, will be published separately.

The material was collected in July and August, 1958 and 1959, and fixed in 1:3 acetic alcohol and modified Carnoy's Fluid (1 part glacial acetic acid, 3 parts absolute alcohol, and 4 parts chloroform). Chromosome counts have been made from the spore mother cells entirely by the squash technique; the counts have been confirmed from a large number of cells in each case. All the photomicrographs are from permanent acetocarmine preparations. Voucher specimens are preserved in the Panjab University Herbarium.

OBSERVATIONS

The course of meiosis in all cases is perfectly normal, except as mentioned below in *A. thelypterioides* and *A.* × *pectinatum*. All the species are sexual, since 64 normal and apparently viable spores were counted within a sporangium in each case except as noted below in *A. thelypterioides*, and apogamy has not been observed in any of them. Both perisporiate and

[14]Beddome, 1892.
[15]Tagawa, 1956, p. 177.
[16]Hooker and Baker, 1874, p. 225.
[17]Hope, 1899, pp. 531, 532.

non-perisporiate spores (cf. *Figs. 3* and *17d*) are present. The spores are broadly perisporiate in eight species, namely, *A. subtriangulare* (and var. *sikkimense*), *A. spinulosum*, *A. Mehrae*, *A. polysporum*, *A. dentigerum*, *A. falcatum*, *A. pectinatum*, and *A. macrocarpum*. The spores of *A. subtriangulare* ($n = 80$) are small; those of the rest are of the same general size. The spores of *A. attenuatum*, *A. Tsaii*, *A. parasnathense*, *A. rupicola*, *A. rubricaule*, *A. Birii*, and *A. himalaicum* are devoid of any clear-cut perisporium. The spores of *A. rubricaule* ($n = 40$) are the largest in this group.

The cytological results are summarized in Table I.[18] It is clear that 15 of these species are diploids, the haploid chromosome number being 40, and that three are tetraploids ($n = 80$). In the *Athyrium* species worked out here, polyploidy has been noted only up to the tetraploid level.

A previous report of the chromosome number of *A. thelypterioides* was by Mehra and Verma[19] who reported both diploid ($n = 40$) and tetraploid ($n = 80$) races. The authors have since studied several populations from the Lachen Valley, 8,000–12,000 feet, in northern Sikkim, also, and noted only the diploid race. Further scrutiny has shown that the tetraploid individuals differ from the true *A. thelypterioides* in the following characters and probably represent a different species:

(1) The individuals are smaller.

(2) The rhizome scales are smaller, and linear in outline, as compared with the larger, linear-lanceolate, broad-based scales of *A. thelypterioides*.

(3) The complete absence of uniseriate fibrillar hairs on the primary and secondary rachises, which is an important charac-

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[18]The names of the species marked * and ** are entirely on the authority of Prof. R. C. Ching.

[19]Mehra and Verma, 1957. The name here used, *Athyrium acrostichoides* (Swartz) Diels (1899), is illegitimate, being a later homonym of *Athyrium acrostichoideum* Bory ex Mérat (1836). The Greek form "*acrostichoides*" and the Latinized form "*acrostichoideum*" are orthographic variants and consequently homonyms; they are exactly comparable to "*pteroides*" and "*pteroideus*," cited as examples of orthographic variants in the International Code of Botanical Nomenclature (Paris Edition, Art. 75, 1956).

FIG. 4, A. DENTIGERUM, SPORE MOTHER CELL, 40 BIVALENTS, × 600. 5, A. SUBTRIANGULARE VAR. SIKKIMENSE, $n = 40$. × 600. 6, A. FALCATUM, $n = 50$. × 600. 11, A. TSAII, SPORE MOTHER CELL, 40 BIVALENTS, × 470. 12, A. THELYPTERIOIDES, SPORE MOTHER CELL, 80 UNIVALENTS, ×470 ter of the species.

(4) The stipes and rachises are straw-coloured and almost naked, a few scales being present at the base only, in strong contrast to the dull-brown stipes, covered with hairs and scales, of *A. thelypterioides*.

(5) The lower pinnae are never reduced to mere auricles as in *A. thelypterioides*.

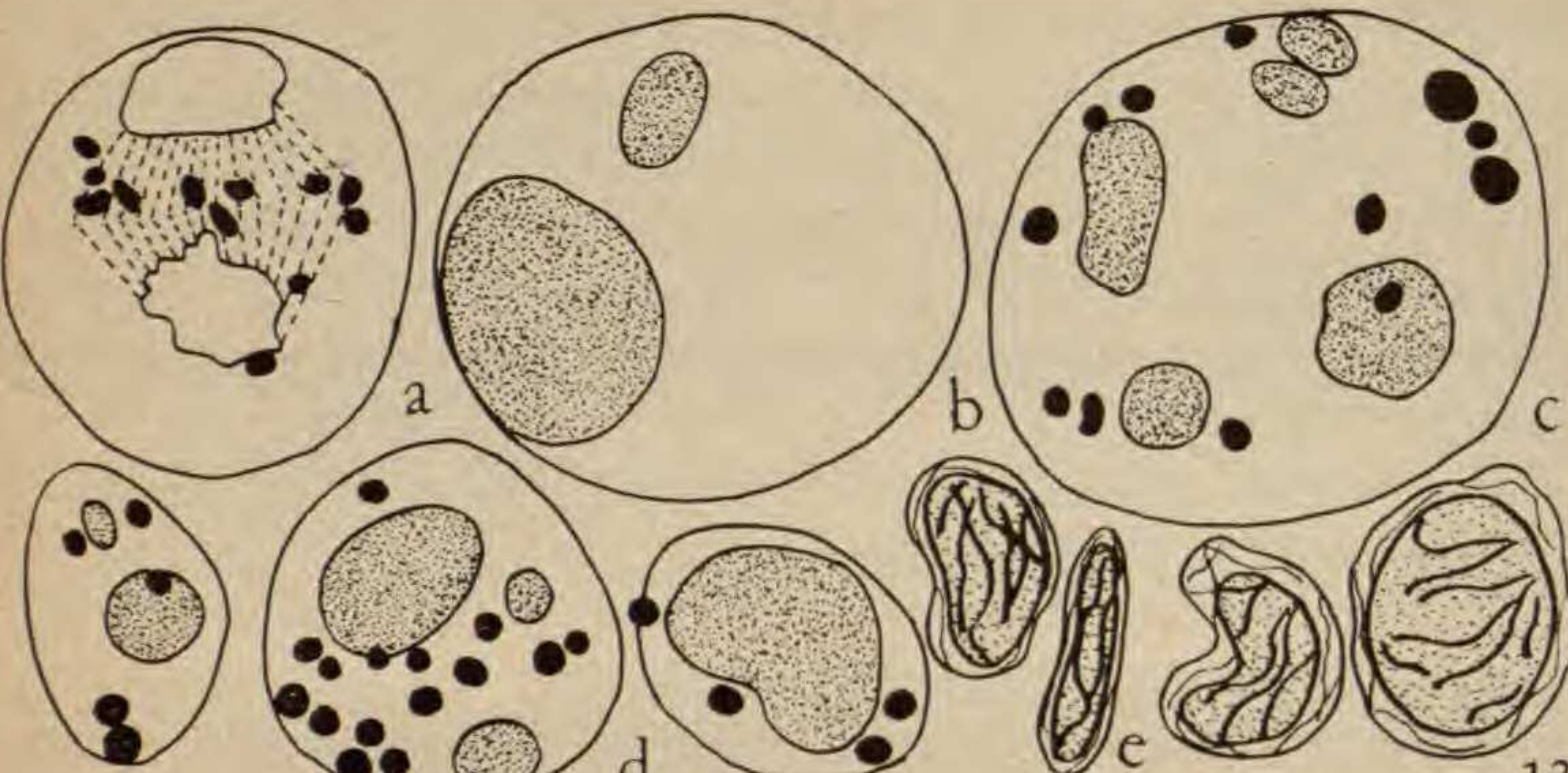
(6) The sori are typically "athyrioid" and not "diplazioid," as in *A. thelypterioides*.

(7) The spores are non-perisporiate rather than broadly perisporiate as in *A. thelypterioides*.

Therefore, in the authors' opinion the tetraploid individuals represent a different species; they are probably very near *A. MacDonellii* Beddome.

The diploid *A. thelypterioides* is morphologically variable. The individuals collected from Tonglu (8,500 feet) and near Thangu (12,000 feet) in the Eastern Himalayas differ from each other in the size of the pinnae and segments, the extent of the marginal crenations, the texture of the blade, and the amount of hairs and scales.

In the Mussoorie area the species is extremely rare and no sexual race has been found. All the individuals of *A. thelypterioides* growing near Dhanolti, 7,000 feet, Mussoorie, are cytologically abnormal. There are no signs of chromosome pairing in any of the spore mother cells, and at late diakinesis 80 univalents were clearly seen (*Fig. 12*). The chromosomes are longish and mitotic in appearance, and show median or submedian constrictions; soon, however, they become contracted and ovoid. The further course of meiosis is highly abnormal. The metaphase plate is seldom properly organized, and the univalents lie scattered in the cell. At A-I, the univalents divide longitudinally and the daughter chromatids reach either of the poles or may be left undivided and remain as laggards which are ultimately organized into micronuclei (*Fig. 13a*). The two nuclei resulting from the first meiotic division may be irregularly shaped and sometimes highly disproportionate,



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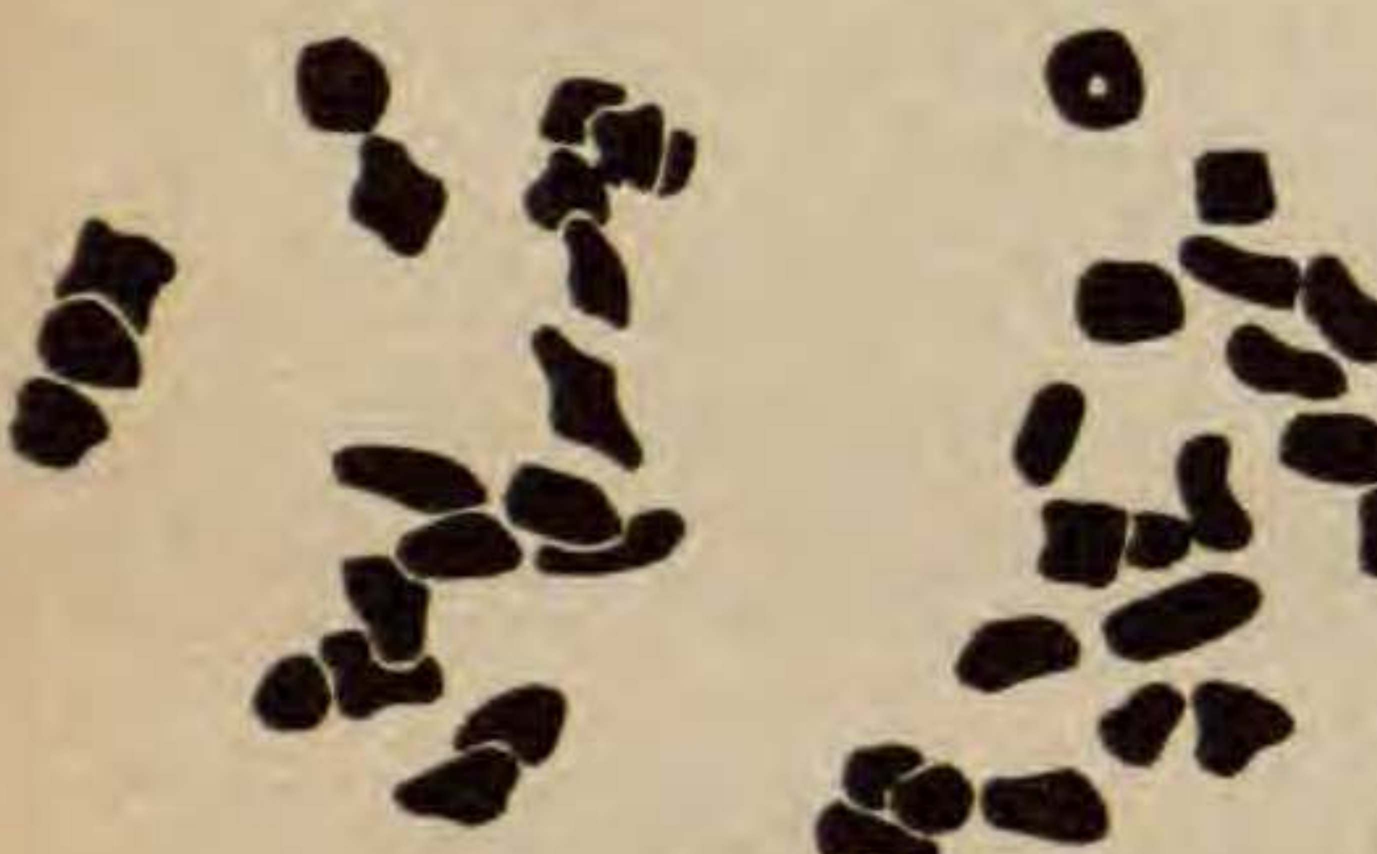

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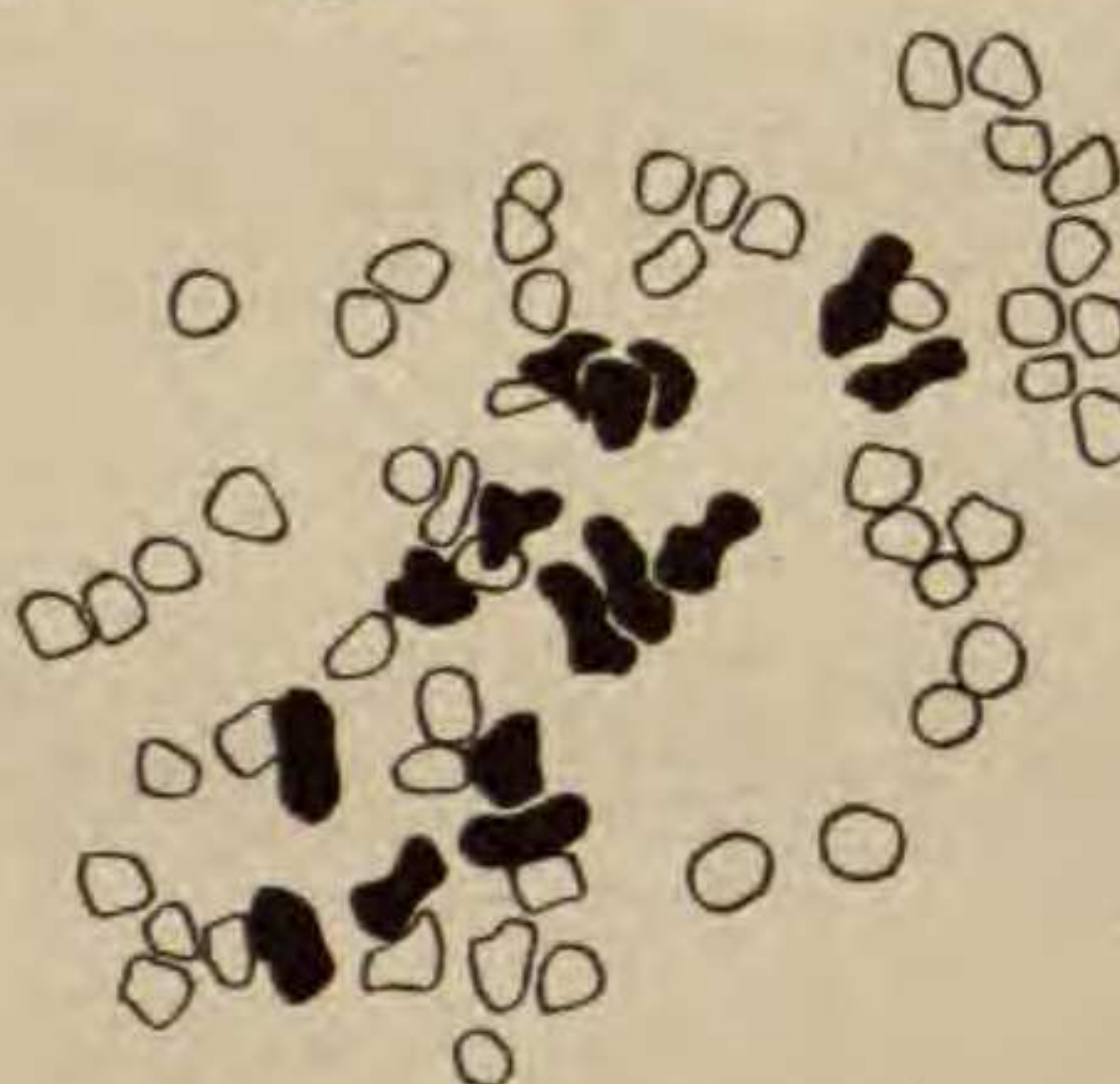
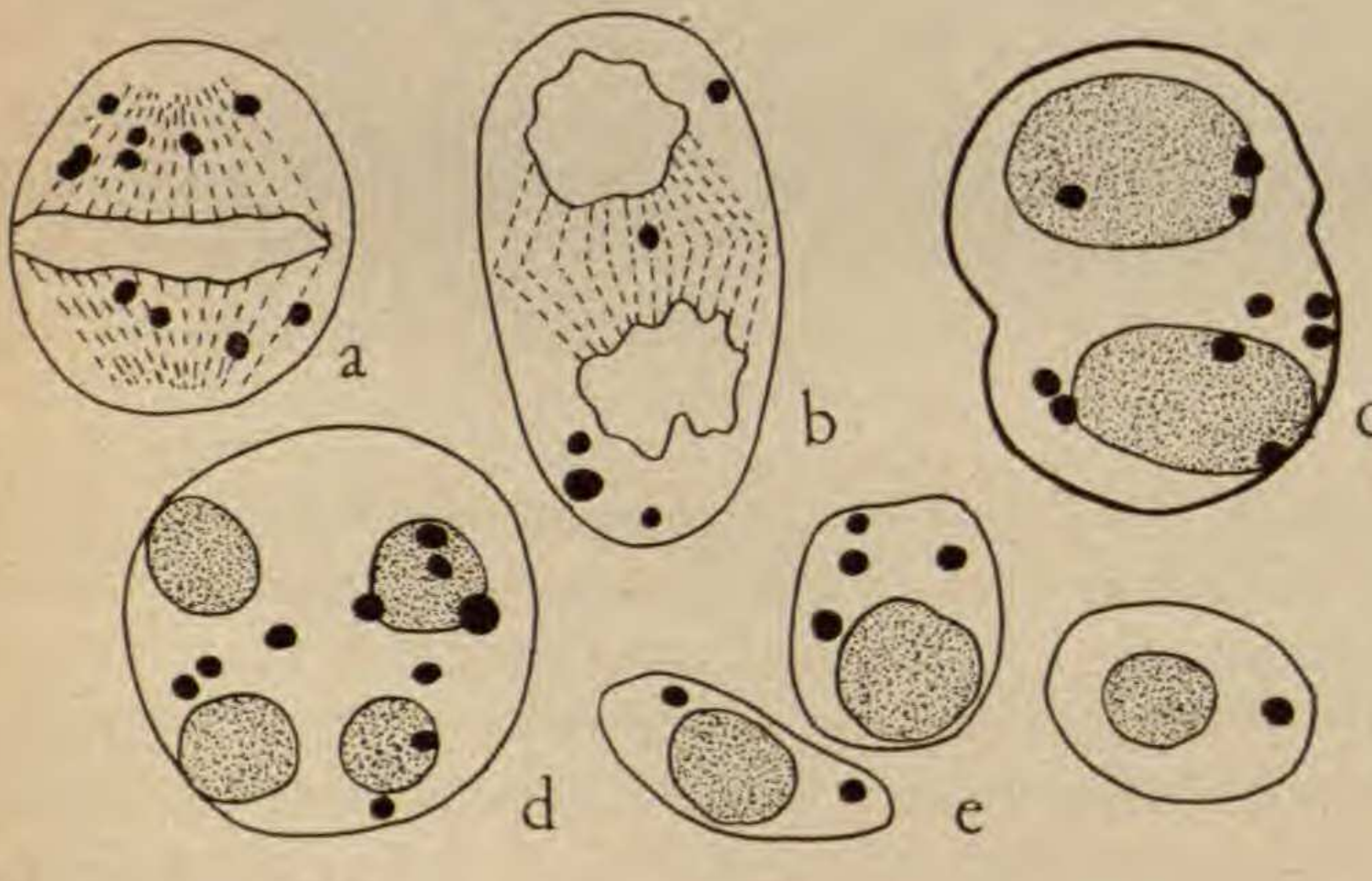


15



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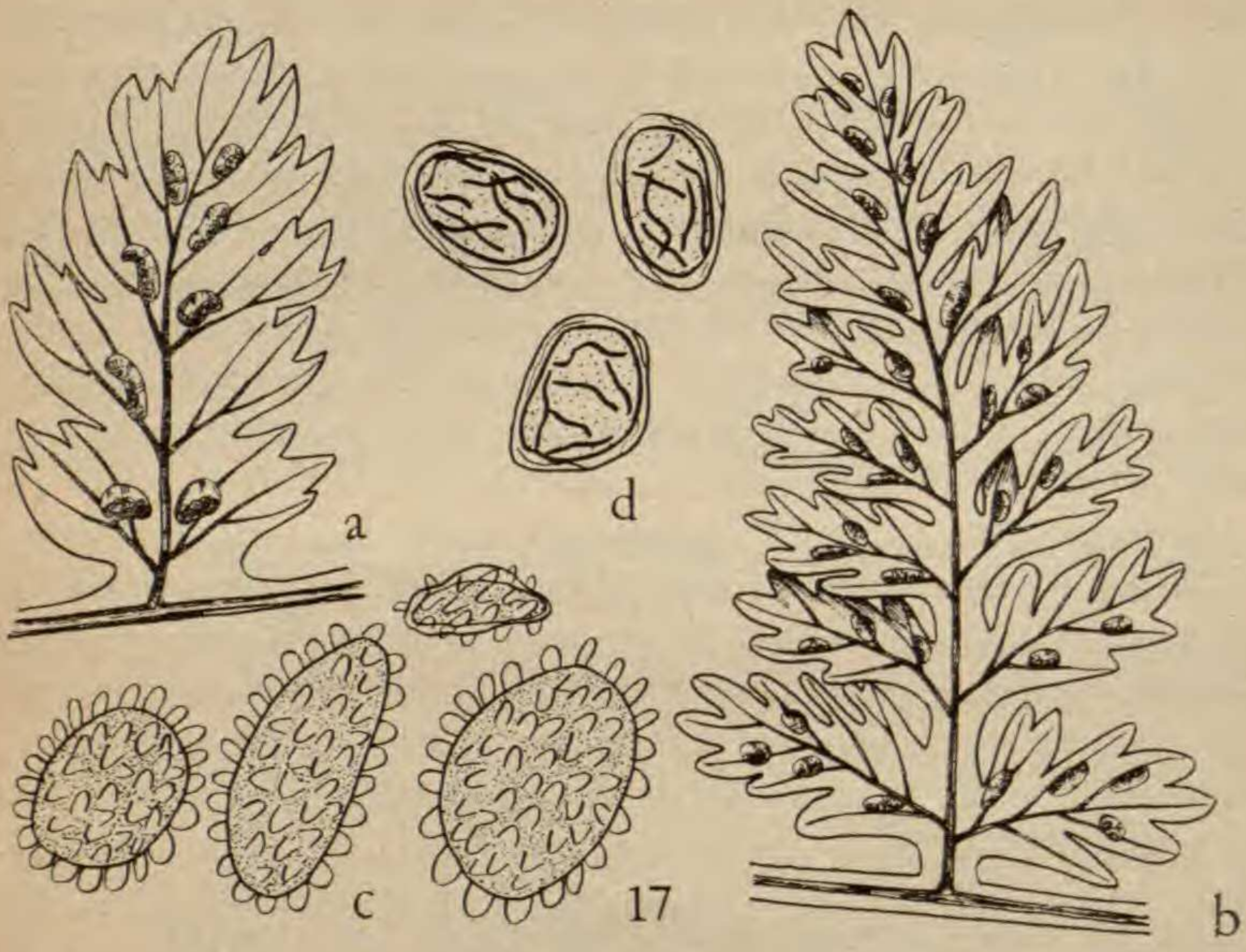
as a consequence of the unequal distribution of the chromatin material (*Fig. 13b*). The homoeotypic division is also irregular. All those univalents that divided in the first division being unable to divide for the second time are left as laggards; at the "tetrad" stage numerous micronuclei are present (*Fig. 13c*). The cytokinesis may be complete or incomplete. The young spores are of variable shapes and sizes and possess micronuclei (*Fig. 13d*). Obviously as a result of these irregularities, the mature spores are unequal in size, some even shrivelled up and abortive (*Fig. 13e*).

Although the Dhanolti (Mussoorie) specimens just mentioned that show abnormal meiosis differ markedly from those of Sikkim (diploid, $n = 40$) in the more elongate, deeply crenate, falcate segments, with a much broader sinus between them, they fall within the range of variation noticed in the species in various regions of the Himalayas. The differences mentioned are probably of little taxonomic importance, and the "sterile" specimens from Dhanolti can hardly be segregated as a variety or form. The almost complete similarity between the sexual and the "sterile" individuals of *A. thelypterioides* leads us to believe that the cytological abnormalities in the Mussoorie populations are not due to hybridity but are of genic origin.

The individuals of the fern designated as *A.* × *pectinatum* in Table I possess characteristically pinkish stipes when fresh. They differ from specimens of *A. pectinatum* from Sikkim, Nainital, and Mussoorie consistently in only two characters: Lamina only bipinnate, with lower pinnae more reduced (tripinnate in *A. pectinatum*) (*Figs. 17a, b*).[20] and spores tuber-

[20]It may be pointed out that these individuals exactly resemble the figure given by Beddome (1863, *t. 154*), for *A. Filix-foemina* from southern India, which later on (Beddome, 1892) was regarded as a small form of *A. Filix-foemina* var. *pectinatum*.

13, A. THELYPTERIOIDES, MEIOSIS; a, ANAPHASE I; b, TELOPHASE I, UNEQUAL NUCLEI; c, "TETRAD," MANY MICRONUCLEI; d, YOUNG SPORES, VARIABLE SIZE, WITH MICRONUCLEI; e, MATURE SPORES; a-d, × 535, e × 225. 15, A. PECTINATUM, $n = 40$, × 800. 15, A. × PECTINATUM, $2n = 80$, I.E. 15 (II) AND 50 (I), × 800. 16, IBID., MEIOSIS; a, METAPHASE I; b, ANAPHASE I; c, BINUCLEATE SPORE, MANY MICRONUCLEI; d, TETRAD, MICRONUCLEI; e, YOUNG SPORES, MICRONUCLEI; ALL × 540



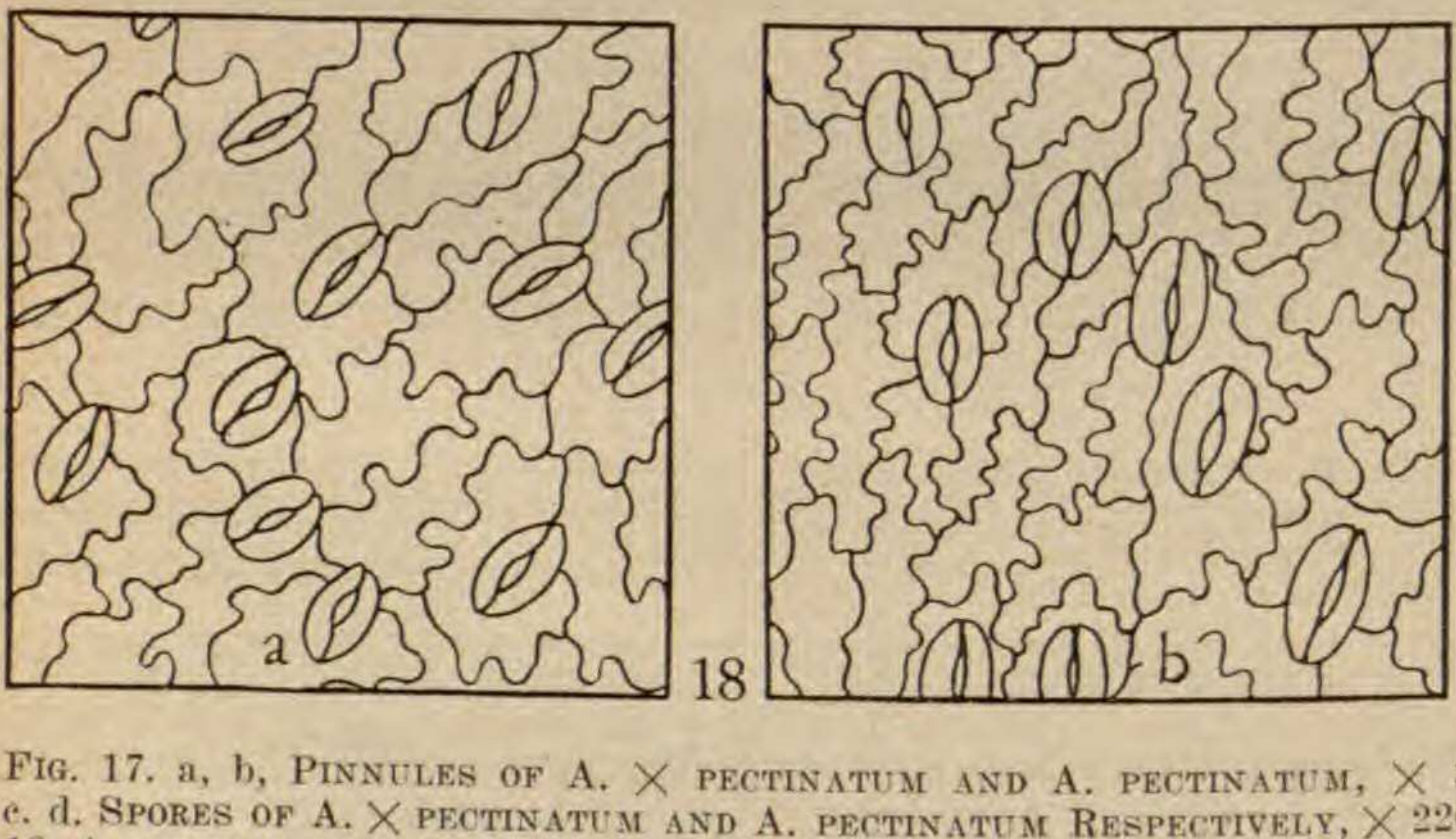


FIG. 17. a, b, PINNULES OF A. × PECTINATUM AND A. PECTINATUM, × 3. c. d. SPORES OF A. × PECTINATUM AND A. PECTINATUM RESPECTIVELY, × 220. 18. A. ATTENUATUM, LOWER EPIDERMIS WITH STOMATA, a, DIPLOID, b, TETRAPLOID, ×85

culate-thickened on the surface (smooth perisporium in *A. pectinatum*) (*Figs. 17c, d*). In this fern the course of meiosis is highly irregular. In the majority of the cells only a partial pairing of the chromosomes is noticed at diakinesis. One such cell is reproduced in *Fig. 15*, which shows $15_{II} + 50_{I}$, giving $2n = 80$. M-I and A-I are also abnormal and laggards are common (*Figs. 16a, b*). Very rarely, the second division fails and a binucleate spore results (*Fig. 16c*). The four nuclei at the tetrad stage are often unequal and numerous micronuclei are organized (*Fig. 16d*). The cytokinesis is irregular, resulting in spores of unequal size with micronuclei (*Fig. 16e*); these are abortive. Unlike other species of *Athyrium* from the Himalayas, these show tuberculate thickenings on the surface (*Fig. 17c*), in which character they resemble those of *Diplazium japonicum* (Thunb.) Beddome, although morphologicially there is no similarity whatsoever between *D. japonicum* and *A.* × *pectinatum*. Therefore at present nothing can be inferred regarding the other parent of this hybrid.

Only one species, *A. attenuatum*, shows intraspecific polyploidy. Diploid and tetraploid individuals grow side by side, but although the smallest individuals of the diploid race are shorter than the smallest tetraploids, morphologically the two races are similar in leaf outline; there are hardly any quantitative differences that could be detected, either in the size of the pinnae or their segmentation. The spores do show differences in size and in the quantity of stored food material, the diploids being smaller and less filled with food material than the tetraploids (*Figs. 3a, b*). There is a little difference in stomatal sizes, the stomata of the tetraploids being slightly bigger. The number of stomata per unit area in the tetraploid is lesser than in the diploid (*Fig. 18a, b*). The epidermal cells of the tetraploid are somewhat larger.

Another species that draws one's attention is *A. subtriangulare*. The typical variety ($n = 80$), with fronds 50–70 cm. long and 20–40 cm. wide, grows at lower elevations than var. *sikkimense*, which is diploid ($n = 40$), with fronds only up to

25 cm. long and 12 cm. wide. Curiously enough the variety, although only diploid, has spores somewhat larger than the typical variety, which may very well speak for its separate identity.

The phenomenon of apogamy, aside from the classical examples, *A. Filix-foemina* var. 'Clarissima Jones,' var. 'Clarissima Bolton,' and var. 'Uncoglomeratum' Stansfield,[21] has not been noticed in any of the 38 species worked out so far, which disproves Mahabale's observation that most species of *Athyrium* are apogamous. Both the examples of apogamous Athyriums worked out by Manton (1953) from Ceylon, *A. maximum* and *A. pinnatum*, are Diplaziums as that genus is now understood with the present day availability of chromosomal information. The names of these ferns are *Diplazium maximum* (Don) C. Chr. and *D. silvaticum* (Bory) Swartz respectively.

DISCUSSION

A regional analysis of all the species thus far worked out is presented in Table II.[22] For the purpose of calculations, species with two cytological races have been counted on the higher side of ploidy. This Table shows that three sexual species have been found with different cytological races—*A. attenuatum* (2x and 4x, from the Himalayas), *A. gymnogrammoides* (4x and 6x, from Ceylon), and *A. macrocarpum* (2x from the Himalayas, 4x and 6x in Ceylon). No major morphological differences are evident in *A. attenuatum*, but the 4x and 6x individuals of *A. gymnogrammoides* are markedly different from each other, as has been illustrated by Manton and Sledge;[23] nothing can be said about *A. macrocarpum* until a thorough comparison of Himalayan and Ceylonese specimens is made.

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[21]Farmer and Digby, 1907.

[22]The information included in this table and the subsequent ones is based on Manton, 1950, 1953, 1954; Britton, 1953; Manton and Sledge, 1954; Wagner, 1955; Mehra and Verma, 1957; Brownlie, 1958; Bir, 1959; and the present investigation.

[23]Manton and Sledge, 1954. It may be mentioned that the taxonomic status of *A. gymnogrammoides*, which belongs to a group of species allied to *A. solenopteris*, is confused, and it can not be said whether the 4x and 6x individuals fall within the boundaries of the species or not.

TABLE I.

Name	Locality and altitude	*n* chromosome number	Fig. no.	Ploidy
Athyrium attenuatum (Clarke) Tagawa	Simdong, N. Sikkim, 11,000′	40	1	Diploid
Athyrium attenuatum (Clarke) Tagawa	Simdong, N. Sikkim, 11,000′	80	2	Tetraploid
**A. Birii* Ching (mss.)	Near Lachen, N. Sikkim, 8,000′	40		Diploid
A. dentigerum (Clarke) Mehra et Bir	Dhanolti, Mussoorie, 7,000′	40	4, 7	Diploid
A. falcatum Beddome	Nainital, 6,000′	40	6, 8	Diploid
A. aff. *flabellulatum* (Clarke) Tard.	Lachen, N. Sikkim, 8,500′	40		Diploid
**A. himalaicum* Ching (mss.)	Lachen, N. Sikkim, 8,500′	40		Diploid
A. macrocarpum (Blume) Beddome	Darjeeling, 7,000′	40		Diploid
A. Mehrae Bir	Near Thangu, N. Sikkim, 12,000′	40	9	Diploid
***A. parasnathense* (Clarke) Ching	Lachen, N. Sikkim, 8,500′	40		Diploid
A. pectinatum (Wall.) Presl	Sainji, Mussoorie, 3,000′	40	14	Diploid
A. pectinatum (Wall.) Presl	Chungthang, N. Sikkim, 6,000′	40		Diploid
A. x *pectinatum* (Wall.) Presl	Magra, Mussoorie, 6,000′	15(II) + 50(I)	15	Diploid hybrid
***A. polysporum* (Clarke) Ching	Lachen, N. Sikkim, 8,500′	80		Tetraploid
A. rubricaule (Edgw.) Bir	Lachen, N. Sikkim, 8,500′	40		Diploid
A. rupicola (Hope) C. Chr.	Near Lachen, N. Sikkim, 8,500′	40		Diploid
A. Schimperi Moug.	Near Chungthang, N. Sikkim, 6,000′	40		Diploid
A. subtriangulare (Hook.) Beddome	Thangu, N. Sikkim, 13,000′	80		Tetraploid
A. subtriangulare var. *sikkimense* Bir	Above Thangu, N. Sikkim, 14,000′	40	5	Diploid
A. spinulosum (Maxim.) Milde	Thangu, N. Sikkim, 13,000′	80	10	Tetraploid
**A. Tsaii* Ching (mss.)	Simdong, N. Sikkim, 11,000′	40	11	Diploid

* New species, discovered by S. S. Bir during the present investigation, as named by Prof. R. C. Ching.

** New combinations (Ching, ined.).

TABLE II. REGIONAL TABULATION OF DIPLOID, TETRAPLOID, AND HEXAPLOID ATHYRIUMS

Himalayas	Ceylon	Europe	North America (Ontario and Michigan)
	Diploid		
thelypterioides (syn. *acrostichoides*)		*Filix-foemina*	*Filix-foemina* var. *Michauxii*
Atkinsonii var. *Andersonii*		*alpestre*	*thelypterioides*
attenuatum, p.p.		*flexile*	*pycnocarpon*
Birii			
Boryanum			
dentigerum			
falcatum			
fimbriatum			
flabellulatum			
aff. *flabellulatum*			
foliolosum			
himalaicum			
macrocarpum			
Mehrae			
oxyphyllum			
parasnathense			
pectinatum			
proliferum			
rubricaule			
rupicola			
Schimperi			
setiferum			
Tsaii			
tenuifrons (= *Clarkei*)			
subtriangulare var. *sikkimense*			
sp. (called *Leucostegia yaklaensis* Beddome)			
	Tetraploid		
attenuatum, p.p.	*anisopterum*		
anisopterum	*erythrorachis*		
polysporum	*gymnogrammoides*		
spinulosum	*macrocarpum*, p.p.		
subtriangulare			
	Hexaploid		
	gymnogrammoides		
	macrocarpum, p.p.		

Only four instances where the same species occurs in different climates have been investigated. The temperate species *A. thelypterioides* (Himalayas and North America) and *A. Filix-foemina* (Europe and North America) show the same chromosome number, $n = 40$. *Athyrium anisopterum* has $n = 80$ in both the Himalayas and Ceylon, but *A. macrocarpum* shows a higher ploidy in Ceylon, being diploid ($n = 40$) in the Himalayas and tetraploid or hexaploid in Ceylon ($n = 80$ or ca. 120).

Table III, which gives a comparison of cytological data from various regions, shows that the three European and three North American species are all diploid, but that no Ceylon species are diploid, two being hexaploid, two tetraploid, and one a hybrid.

TABLE III. REGIONAL COMPARISON OF CYTOLOGICAL DATA

Region	No. spec. counted	Dipl.	Tetrapl.	Highest polypl.	Hybr.	Percent of dipl.
Himalayas	29[1]	24	5	4x	—	82.74
Ceylon	5	—	2	Two 6x	1	0
Europe	3	3	—	—	—	100
No. Amer.	3	3	—	—	—	100

[1]*A.* x *pectinatum*, from Mussoorie, not included.

In the Himalayas of the 29 species that have been studied, 24 are diploid (82.7%) and 5 are tetraploids. The highest grade of euploidy encountered in the Himalayas is only up to the tetraploid level (as compared with hexaploid in Ceylon), and the preponderance of diploids is significant. The Himalayas are similar to Europe and North America (Ontario and Michigan) in the temperate climate, whereas Ceylon has a tropical climate. Therefore, the above analysis of the situation in *Athyrium* appears to give support to Manton's (1953) observation that, "Evolution is proceeding faster in the tropics than in temperate latitudes."

Whether *Athyrium* has been placed in the subfamily Asplenioideae of the Polypodiaceae,[24] or in the tribe Athyrieae of the Aspleniaceae[25], or the subfamily Athyrioideae of the Dennstaed-

[24]Christensen, 1906, 1938.
[25]Ching, 1940; Dickason, 1946.

TABLE IV. COMPARISON OF CYTOLOGICAL DATA FOR ATHYRIUM WITH ALLIED GENERA

Genus	No. of species	No. of species counted	Basic no.	Dipl.	Tetrapl.	Highest polypl.	Hybr.	Apogamy	Percent of dipl.
Athyrium[1]	180	38	40	27	8	Two 6x	1	—	71
Diplazium[2]	380	27	41	11	8	Two 6x	One 5x	Four 3x One 5x	40.74
Diplaziopsis[3]	2	1	41	1	—	—	—	—	—
Callipteris[4]	4	1	41	1	—	—	—	—	—
Cornopteris[6]	13	1	41	—	1	—	—	—	—
Cystopteris	17	10	42	2	4	Two 6x One 8x	One 3x	1	22.25

[1]Data from Manton, 1950, 1953; Mahabale et al., 1953; Britton, 1953; Manton & Sledge, 1954; Wagner, 1955; Mehra & Verma, 1957; Bir, 1959, and present investigation.
[2]Manton, 1953, 1954; Manton & Sledge, 1954; Brownlie, 1958; Bir, 1959, and Bir ined.
[3]Bir, 1958.
[4]Manton, 1954 (under name *Athyrium accedens*).
[5]According to Copeland, 1947.
[6]Bir, ined.
[7]Manton, 1950; Britton, 1953; Wagner, 1955; Bir, ined.

tiaceae,[26] or in the family Aspidiaceae,[27] or recently in a separate family Athyriaceae,[28] it has usually been grouped with *Cystopteris* Bernh., *Diplaziopsis* C. Chr. *Diplazium* Swartz, *Cornopteris* Nakai, and *Deparia* Hook. & Grev. Kept separate by Ching, *Diplazium, Cornopteris,* and *Deparia,* were merged with *Athyrium* by Copeland, who on the other hand maintained Bory's genus *Callipteris,* which is not done by other authors. *Callipteris* was based on *C. prolifera* (Lam.) Bory, which is *Diplazium proliferum* (Lam.) Thouars [*Athyrium accedens* (Blume) Milde, of Holttum's treatment[29]]. The cytological data on these genera, which for the purposes of this discussion are treated separately, is presented in Table IV. The number of species referred to each genus follows Ching's estimate,[30] except for *Callipteris.*

The data in Table IV show that the basic chromosome numbers of these genera are 40, 41, or 42. The larger numbers may have evolved through aneuploidy. *Deparia,* a monotypic genus endemic to Hawaii, has not been studied yet. *Diplazium* seems to be actively evolving compared to *Athyrium,* because of the comparatively lower percentage of diploids, the greater number of hybrids and the consequent establishment of apogamy. The few hybrids recorded, the higher percentage of diploids, and the almost total absence of apogamy reveals that from an evolutionary viewpoint *Athyrium* is a static genus in this respect, and that evolution in it is principally by genic mutations.

SUMMARY

Chromosome counts of 16 species of *Athyrium* from the Himalaya Mountains show that 13 species are diploid ($n = 40$), and 3 tetraploid ($n = 80$). All are sexual, apogamy being absent. Only one species, *A. attenuatum,* shows intraspecific polyploidy (diploid and tetraploid races). The counts of 29 species of the genus known from the Himalayas show that 82.74% are diploids and only 17.26% tetraploids, a significant abundance of diploids

[26]Holttum, 1949, 1954.
[27]Copeland, 1947.
[28]Alston, 1956.
[29]Holttum, 1954.
[30]Ching, 1940.

compared with data from Ceylon. From comparisons with allied genera, especially *Diplazium*, it is abundantly clear that *Athyrium* is a static genus as far as evolution by hybridization and polyploidy is concerned.

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REFERENCES

ALSTON, A. H. G. 1956. The Sub-division of the Polypodiaceae. *Taxon* 5: 23–25.

BEDDOME, R. H. 1863. The Ferns of Southern India. Gantz Brothers, Madras.

—. 1892. A Handbook to the Ferns of British India, Ceylon, and the Malay Peninsula, with Supplement. Thacker, Spink, and Co., Calcutta.

BIR, S. S. 1958. Cytology of Diplaziopsis javanica. *Curr. Sci.* 27: 146.

—. 1959. Cytotaxonomic Notes on Some Aspleniaceae from Kulu Valley. *Journ. Ind. Bot. Soc.* 38: (In press).

BOWER, F. O. 1928. The Ferns. Volume III. Cambridge University Press.

BRITTON, D. M. 1953. Chromosome Studies on Ferns. *Amer. Journ. Bot.* 40: 575–583.

BROWNLIE, G. 1958. Chromosome Numbers in New Zealand Ferns. *Trans. Roy. Soc. New Zealand* 85: 213–216.

CHING, R. C. 1940. On the Natural Classification of the Family Polypodiaceae. *Sunyatsenia* 5: 201–270.

CHRISTENSEN, C. 1906. Index Filicum. Copenhagen.

—. 1938. Filicinae, in Verdoorn, *Manual of Pteridology.* pp. 522–556. The Hague.

CLARKE, C. B. 1880. A Review of the Ferns of Northern India. *Trans. Linn. Soc. London, II, Bot.* 1: 425–611.

COPELAND, E. B. 1947. Genera Filicum. Waltham, Massachusetts, U. S.

DICKASON, F. G. 1946. A Phylogenetic Study of the Ferns of Burma, and The Ferns of Burma. *Ohio Journ. Sci.* 46: 73–141.

FARMER, J. B. and DIGBY, L. 1907. Studies on Apospory and Apogamy in Ferns. *Ann. Bot.* 21: 161–200.

HOLTTUM, R. E. 1949. The Classification of Ferns, *Biol. Rev.* 24: 267–296.

—. 1954. Flora of Malaya, Vol. II. Ferns. Government Press, Singapore.

HOOKER, W. J. and BAKER, J. G. 1874. Synopsis Filicum, ed. 2. London.
HOPE, C. W. 1899–1904. The Ferns of North-western India. *Journ. Bomb. Nat. Hist. Soc.* **12**: 527–538, 621–633; **13**: 25, 26, 236–251, 443–461, 657–671; **14**: 119–127, 252–266, 458–480, 720–749; **15**: 67–111, 415–429.
MAHABALE et al. 1953. Life History of Athyrium Hohenackerianum Bedd. *Proc. Ind. Sci. Congr. Abst.* **40**: 86.
MANTON, I. 1950. Problems of Cytology and Evolution in the Pteridophyta. Cambridge University Press.
—. 1953. The Cytological Evolution of the Fern Flora of Ceylon. *Symposia Soc. Exper. Biol. No. 7, Evolution.* pp. 174–185.
—. 1954. Cytological Notes on One Hundred Species of Malayan Ferns. Appendix to R. E. Holttum, Flora of Malaya, Vol. II. Ferns. Singapore.
MANTON, I. and SLEDGE, W. A. 1954. Observations on the Cytology and Taxonomy of the Pteridophyte Flora of Ceylon. *Phil. Trans. Roy. Soc. London,* Ser. B, **238**: 127–185.
MEHRA, P. N. and VERMA, S. C. 1957. The Cytology of Some Athyrium Species from Northern India. *Ann. Bot.,* n. ser., **21**: 455–459.
TAGAWA, M. 1956. Occasional Notes on Asiatic Pteridophytes, 7. *Acta Phytotax. Geobot.* **16**: 174–178.
WAGNER, W. H., Jr. 1955. Cytotaxonomic Observations on North American Ferns. *Rhodora* **57**: 219–240.

BOTANY DEPARTMENT, PANJAB UNIVERSITY, AMRITSAR, INDIA.

Notes and News

FERN PHOTOGRAPHS.—An article entitled "A Technique for Close-Up Photography of Freshly-Collected Fertile Fern Specimens," by Charles Neidorf, appeared in the August and September, 1960, numbers of Turtox News, published by the General Biological Supply House, Inc., Chicago, Illinois. Included as illustrations for the article are reproductions of two of the author's fern photographs. On a number of occasions[1] the American Fern Journal has published other examples of Mr. Neidorf's work. The photographs are notable for the amount of detail (some of it inevitably lost in the reproductions) revealed in the shape, arrangement and structure of the sori, indusia, sporangia, glands, scales, etc., details which are characteristic of the various species. Many of the photographs are quite striking in appearance and would be suitable for framing